

A NEW *VOLVATELLA* (MOLLUSCA: ASCOGLOSSA) FROM BERMUDA, WITH COMMENTS ON THE GENUS

Kerry B. Clark

ABSTRACT

A new species of *Volvatella*, *V. bermudae*, is described from eastern Bermuda. Major diagnostic features of the species include a flattened head and displaced, rotated and inverted buccal mass, a siphonal canal with a length of about one-third the total shell length, a thick rigid shell, and apparent symbiotic retention of intact algal chloroplasts. The new species lives epifaunally upon its food alga, *Caulerpa racemosa* (Forsskål) Agardh.

Using conchological characteristics, only five other species of *Volvatella* can be reliably separated at present: *V. fragilis* Pease, 1860; *V. vigourouxii* (Montrouzier, 1861); *V. candida* Pease, 1868; *V. viridis* Hamatani, 1976; and *V. elioti* (Evans, 1950). The genus *Volvatella* exhibits digestive gland anatomy intermediate between that of *Ascobulla* and the Elysiidae, supporting the concept of *Volvatella* as the basal stock for adaptive radiation in the Ascoglossa. The appearance of functional symbiotic chloroplasts in the Ascoglossa apparently correlates with the transition from burrowing to epifaunal forms, as exhibited by various members of the genus *Volvatella* (burrowing forms are generally white, epifaunal forms green).

The genus *Volvatella* has been accepted by most authors as near the basal stock of the order Ascoglossa (Boettger, 1963; Kay, 1968; Clark and Busacca, 1978; Thompson, 1979). Unfortunately, the genus is poorly known. About 11 species of *Volvatella* have been described (Thompson, 1979), but several of these are probably synonyms. Most of these were described only by shell characteristics, or with very brief descriptions of soft parts. Baba (1966) and Thompson (1979) provide the only reasonably complete descriptions of *Volvatella* anatomy. Even less is known about the ecology of the genus; only Thompson (1979) describes much of the biology of the living animal.

Volvatella has been found widely in the tropical Indo-Pacific, and recently in the extreme eastern Atlantic (Thompson, 1979). The species described here is the first record of the genus in the west Atlantic.

SUPERFAMILY OXYNOACEA

Family Volvatellidae

Genus *Volvatella* Pease, 1860

Volvatella bermudae, new species

Diagnosis.—Shell bulloid, with broad aperture; posterior of aperture extended to form siphonal canal and spout. Periostracum thick, strong, extending beyond thick inner calcareous layer. Left margin of aperture recurved; left margin of siphonal aperture reflected to form a shelf, with calcareous callus; sides of siphonal canal not overlapping; canal nearly parallel to longitudinal axis of aperture, extending beyond body whorl. Buccal mass anteroposteriorly inverted and dorsoventrally flattened, with consequent displacement of salivary glands, buccal ganglion, buccal nerve, salivary glands, and esophagus. Radula with approximately 8 ascending teeth, 18 descending, 1 preradular tooth; radular teeth with about 16-18 denticles per side. Penial stylet about 130 μ m, tubular, with expanded proximal portion. Size at maturity 5-6 mm. Mantle green, body white.

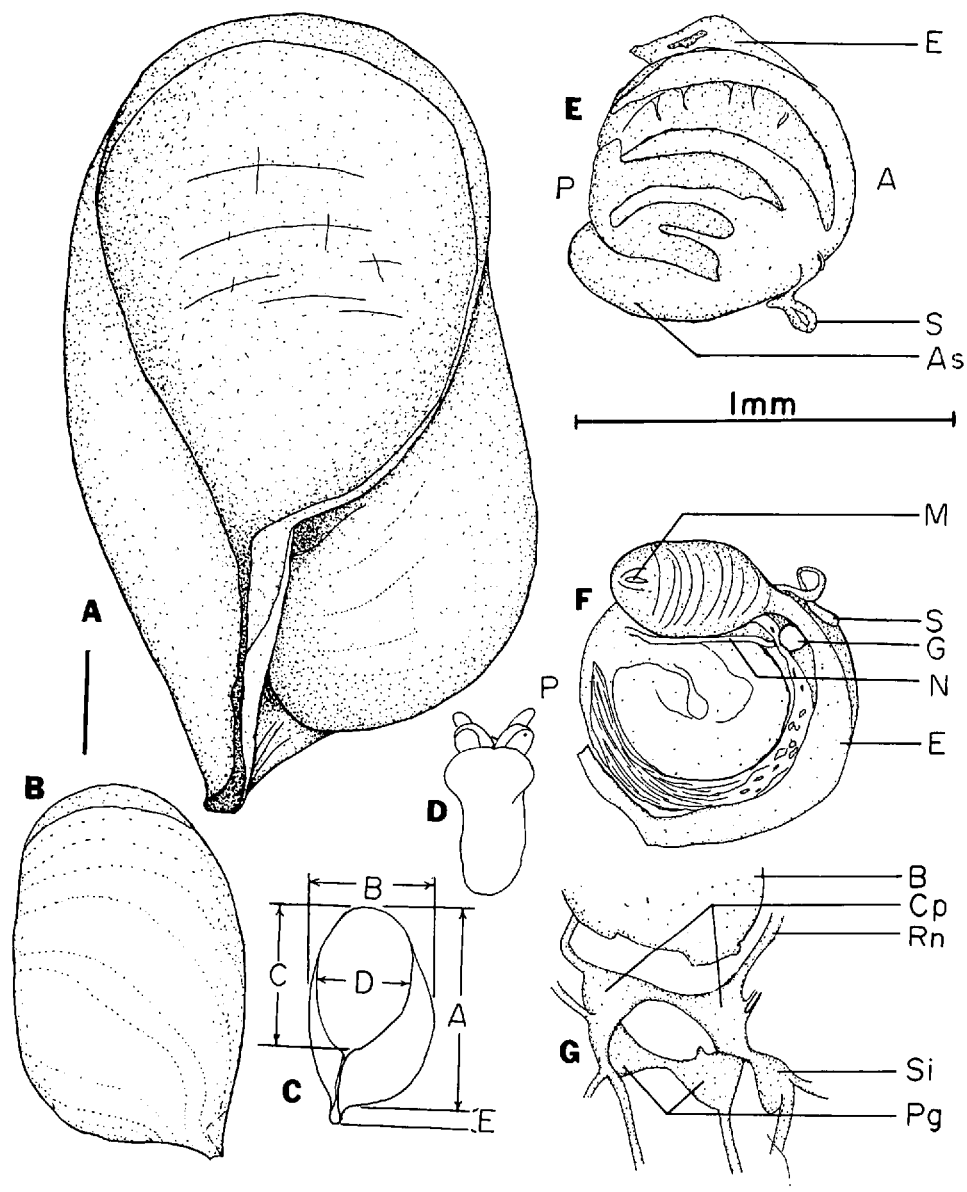


Figure 1. *Volvatella bermudae*. A-D: A, Ventral view of shell; B, Dorsal view of same shell; C, Measurements used in Table I; D, Ventral view of relaxed animal. (Scale line = 1 mm; B and D are $\frac{1}{2}$ magnification of A). Internal anatomy of *Volvatella bermudae* E-G. E, Dorsal view of buccal mass; F, Ventral view of buccal mass; G, Central nervous system. Abbreviations: A—anterior; P—posterior; E—esophagus; S—salivary gland; As—ascus; M—mouth; G—buccal ganglion; N—buccal nerve; B—buccal mass; Cp—cerebropleural ganglia; Rn—rhizophoral nerve; Si—supraintestinal ganglion; Pg—pedal ganglia.

Table 1. Shell measurements of *Volvatella bermudae* (refer to Fig. 1C) (All measurements are in mm)

Specimen	Length (A)	Width (B)	Apert. L (C)	Apert. W (D)	Spout L (E)
1	3.35	2.06	2.77	1.61	0.06
2	3.35	2.13	2.52	1.61	0.23
3	4.52	2.84	3.10	2.52	0.19
4	5.97	4.10	3.93	2.45	0.58
5	6.45	4.19	4.26	2.84	0.26
6	6.64	4.00	4.19	2.45	0.32
7	7.48	5.10	4.68	2.45	0.65
Mean ratio	(1.00)	.64	.69	.44	.06

Material Examined.—Approximately 50 specimens were collected live from several locations in eastern Bermuda: Tobacco Bay, Ferry Reach, Whalebone Bay, and Bailey's Bay. Three preserved specimens were partially dissected, and two specimens were sectioned. The holotype (USNM 795118) and paratype (USNM 795119) were collected from Tobacco Bay (latitude 32°23'15"N; longitude 64°40'40"W), 20 August 1979.

Description.—The shell of *V. bermudae* is constructed of an outer yellowish-green periostracum and an inner white calcareous layer. The periostracum overlaps the calcareous layer, extending anteriorly as a tough, horny membrane (Fig. 1A, B). The calcareous layer is rigid and fairly strong, though brittle and tending to crack when handled roughly; together, the two layers form a surprisingly strong shell. The left margin of the shell recurves, forming a rolled lip, and widens along the siphonal canal to form a flat, flangelike lip; the calcareous layer reflects over the periostracum here to form a callus (Fig. 1A). This lip contacts the inflated posterior portion of the body whorl to form a long umbilicus. The siphonal canal extends a short distance beyond the body whorl; the axis of the canal is nearly parallel to the longitudinal axis of the shell. The total length of the canal is about $\frac{1}{3}$ of the total shell length; other shell characteristics are summarized in Table 1. The mantle, containing densely ramified diverticula of the digestive gland, is visible through the shell as a dark green layer; analysis by ultraviolet epifluorescence showed that these ducts contained many apparently intact chloroplasts of *Caulerpa racemosa*.

The head was usually held inside the shell margin, hence was difficult to study in the living animal. The rhinophores, when fully extended, were conical (Fig. 1D), but were usually somewhat contracted as low crests. The head is relatively small and flat. Hancock's organ is apparently absent. On the right side of the head is a thick, muscular penis (usually retracted into a sheath), which bears a cuticular stylet (Fig. 2E, F). The stylet is normally retracted into the penis; because of the thickness of the penis, the stylet is difficult to find in many specimens. The penis is circled by several stout muscular bands, and bears several knoblike processes on the anterior surface.

The propodium is divided into two parts by a longitudinal groove; the metapodium is V-shaped and slightly asymmetrical (Fig. 1D). The mantle cavity opens on the right side near the posterior metapodium, expands dorsally above a membranous shelf (which contains the right pedal retractor muscle), and spirals to the left around the visceral mass. A plicate gill of many folds lines the dorsal surface of the mantle cavity. As Baba (1966) noted in *V. vigourouxii*, the digestive gland forms a large posterior mass, but also gives off ducts which ramify throughout

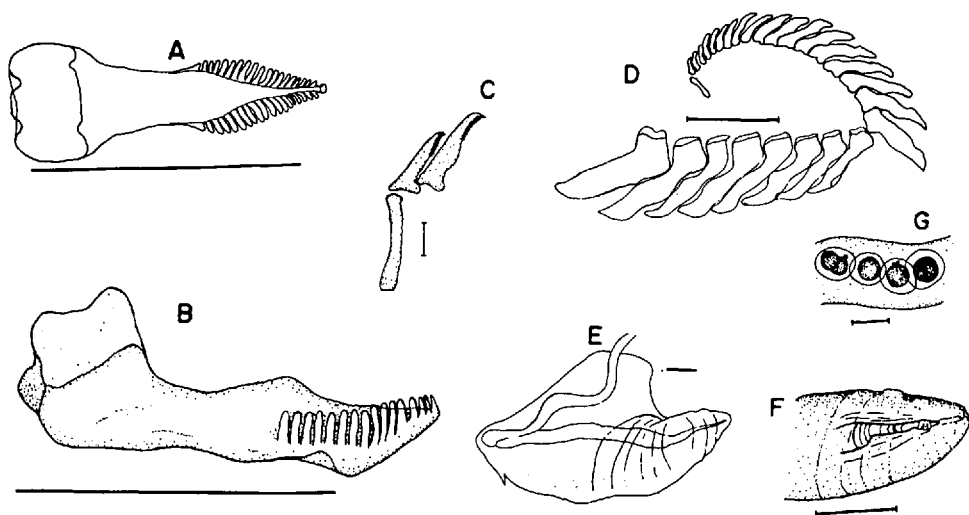


Figure 2. A, Dorsal view of tooth; B, Lateral view of tooth; C, Preradular tooth and first two teeth; D, Radula; E, Penis; F, Distal end of penis and penial stylet; G, Portion of egg string. Scale lines: C—10 μm ; all others—100 μm .

the mantle epithelium. This feature also occurs in *V. laguncula* (Thompson, Fig. 2d). The remainder of the posterior visceral mass was not dissected.

The radula (Fig. 2A–D) is typical of the genus. The base of the tooth (Fig. 2A) is relatively narrow; the tip bears about 15 to 18 fine prongules (denticles). A single preradular tooth is present. The radular teeth gradually increase in size, to a maximum of about 140 μm (Fig. 2D).

The head is somewhat flattened. A displacement of the buccal mass is visible upon dissection (Fig. 1E, F). The normal position in *Volvatella* and other ascoglossans is with the ascus ventral, the radula oriented in the sagittal plane. In *V. bermudae*, the anteroposterior axis is rotated about 150°, the vertical axis 90°, so that the mouth and ascus lie on the right side near the posterior of the buccal mass.

The salivary glands, buccal ganglion and nerve are accordingly displaced; the esophagus exits on the anterior side, loops forward and around the left side, then follows the normal course. The central nervous system (Fig. 1G) shows a slight asymmetry but is otherwise fairly normal.

The cephalic compression and asymmetry are also evident in transverse sections (Fig. 3). The left and right pedal retractor muscles are quite large. Ducts of the digestive gland occur in all areas of the dorsal and lateral mantle.

Habitat and Ecology.—*Volvatella bermudae* is fairly common in the localities examined, but occurs in a quite restricted microhabitat within these sites. It occurred only on *Caulerpa racemosa*, and was found only where the alga grew on vertical rock faces, in areas of strong water circulation, from the upper limit of *Caulerpa* growth to about 3 m depth. In Tobacco Bay, where it was abundant, it occurred together with *Elysia subornata* Verrill, 1901 and *Oxynoe antillarum* Mörch, 1863.

V. bermudae did not adapt well to aquarium culture. Activity declined shortly after collection, and few animals survived more than one week in aquaria, even

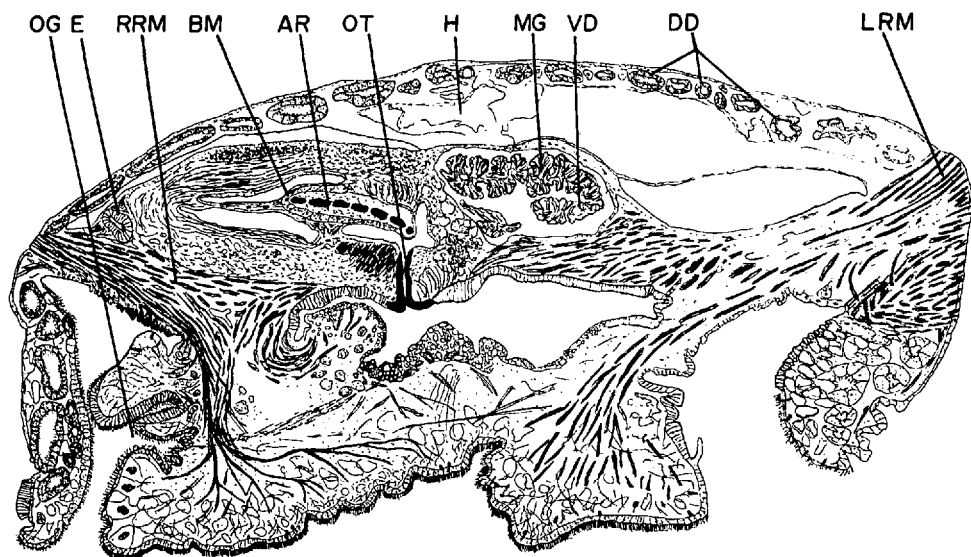


Figure 3. Transverse section of *Volvatella bermudae* through buccal mass. Abbreviations: OG—oviducal groove; E—esophagus; RRM—right pedal retractor muscle; BM—buccal mass; AR—ascending radula; OT—oral tube; H—heart; MG—mucus gland; VD—vas deferens; DD—digestive gland diverticula; LRM—left retractor muscle.

when supplied with running seawater. This contrasts with nearly all other asco-glossans, which usually can be maintained easily.

The observed mortality and habitat restrictions suggest that *V. bermudae* requires strongly circulating water and/or high light intensities. This may relate to the retention of symbiotic chloroplasts by *V. bermudae*; abundant intact plastids have been observed in the digestive diverticula of 24-h-starved animals (Stirts, 1980) (Fig. 4).

The shape of the shell allows a saddle-like attachment to utricles of *C. racemosa*; when the animals are so positioned, they can clamp very tightly to the alga. This behavior prevents dislodgment by strong currents and wave action in the habitat of *V. bermudae*. Possibly the cephalic compression and buccal torsion represent modifications allowing feeding in the "clamped" position; the head was rarely extended beyond the shell margin, except when the animal was actively moving.

Only one animal produced eggs. A single strand of eggs (Fig. 2G) was extruded from the oviducal groove, just above the right side of the head; only about 100 eggs were produced. The eggs were about $66\ \mu\text{m}$ in diameter; albumen was absent. Planktotrophic larvae hatched after about 5 days.

Discussion.—Comparison with other species of *Volvatella* is, as Thompson (1979) noted, hindered by the absence of comprehensive descriptions for most species. However, the shell shape and thickness, the distinctive compression of the cephalic anatomy, and its distribution are adequate to separate *V. bermudae* from all other *Volvatella* species.

The shells of several *Volvatella* species are similar enough to suggest synonymy. These species share the characteristics of an aperture nearly as wide as the shell and slightly less than half the shell length (excluding spout), a straight canal running nearly exactly along the mid-ventral axis of the shell, and a short posterior

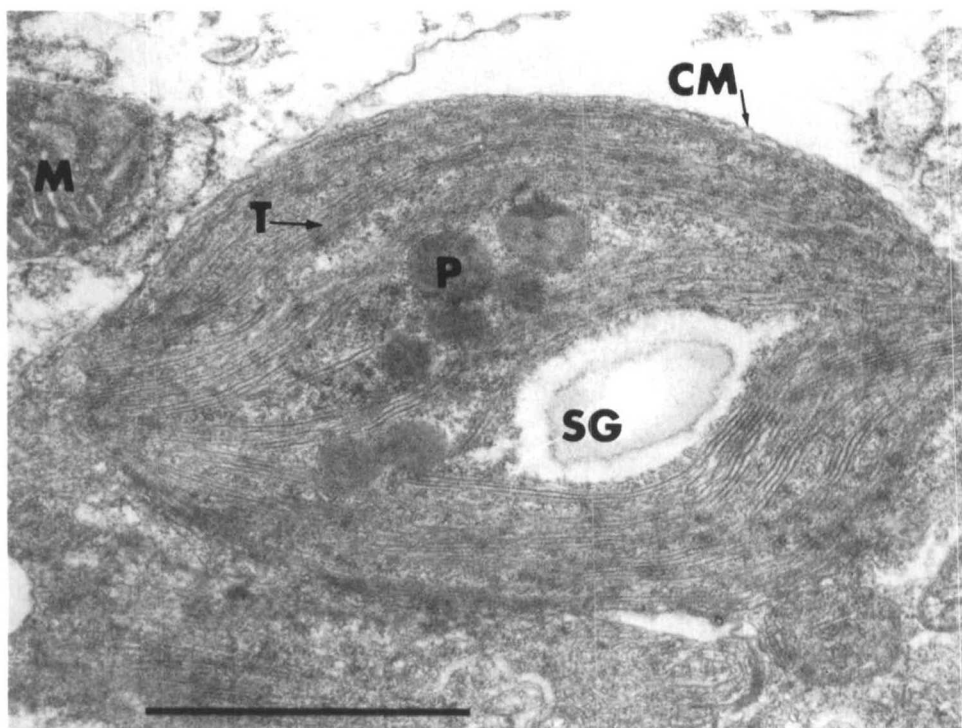


Figure 4. Intact chloroplast in digestive gland cell of 24-h-starved *Volvatella bermudae*. M—host mitochondrion; T—thylakoid; P—plastoglobulus; SG—starch grain; CM—chloroplast membrane. Scale bar equals 1 μ m. (Micrograph courtesy of H. M. Stirts.)

siphon in line with the ventral canal. These species include *Volvatella fragilis* Pease, 1860, from Hawaii, the type of the genus; *V. pyriformis* Pease, 1868, from Polynesia; *V. cincta* Nevill, 1869, from Ceylon; *V. laguncula* Sowerby, 1894, from South Africa; *V. ficula* Burn, 1966, from Fiji; *V. ayakii* Hamatani, 1972, from Japan; and *V. evansi* (Kay, 1961), from Hawaii.

These species also have a "shell" (mantle) color of white (*fragilis*, *ficula*, *laguncula*, *ayakii*), orange (*pyriformis*, *evansi*), (but not green) often with orange or red bands (*ficula*, *pyriformis*, *cincta*, *evansi*). The orange or red bands are absent in *V. ayakii* and *V. laguncula* (Hamatani, 1972; Thompson, 1979). However, the orange or red color suggests carotenoid pigments; as these are often of dietary origin, their presence or absence is of dubious utility as a diagnostic feature. Pease (1868) indicates differences in cephalic appendages for *V. fragilis* and *V. pyriformis*; however, the highly mutable nature of these in *V. bermudae* indicates that these features require confirmation.

Volvatella vigourouxii (Montrouzier, 1861) was redescribed by Baba (1966), and is the most comprehensively described species. It differs from *V. fragilis* group by its narrow aperture, moderately long spout, and elongated, short-based teeth. This species' range includes Japan and New Caledonia. Baba (1966) indicates that *V. kawamurai* Habe, 1946, is a synonym.

V. elioti (Evans, 1950) has a very long, curved spout, a wide aperture greater than half the shell length, and a fairly short canal. Though quite distinct from other *Volvatella*, this species definitely belongs in the genus.

Volvatella viridis Hamatani, 1976, most closely approaches *V. bermudae*. It

shares the features of a green mantle, a spout twisted to the right, wide aperture greater than half the shell length, and a diet of *Caulerpa racemosa* (Hamatani, 1976). However, the base of the radular tooth is less strongly angled from the axis than in *V. bermudae*, the teeth are about half as long, the shell is very thin and flexible, the spout does not project beyond the body whorl, and the canal is twisted to the right rather than parallel to the shell's longitudinal axis. A penial stylet is apparently absent.

V. candida Pease, 1868, has been suggested as a *Cylindrobulla* or *Ascobulla* (Thompson, 1979). If so, a spiral apical groove should have been noted (but was not); the shell shape, excluding the apical groove, appears intermediate between the typical volvatellid and the cylindrobullid forms, possibly representing a very primitive *Volvatella*, lacking a posterior spout.

The structure of the digestive gland in *Volvatella* provides an interesting transition between the more primitive *Ascobulla* and the elysiiform *Ascoglossa*. In *Ascobulla*, *Oxynoe*, and *Lobiger*, only a central massive digestive gland is present, while both a central mass and pallial diverticula are present in *Volvatella*. In the Elysiidae, the central mass is totally lost, and all functions transferred to the pallial diverticula. This series supports the hypothesized position of *Volvatella* as the basal stock of the modern *Ascoglossa* (Boettger, 1963; Kay, 1968; Clark and Busacca, 1978; Thompson, 1979). The form of the digestive gland in the Oxynoidae, Lobigeridae, and Juliidae can also be related to *Volvatella*. In *Oxynoe* and *Lobiger*, considered on other bases to be more advanced than *Volvatella*, the pallial diverticula have apparently been suppressed, while in the Juliidae, the pallial diverticula are retained to a slight degree (Baba, 1966). If the plastids in *Volvatella* do prove to be functional, then the evolutionary path of chloroplast symbiosis in the *Ascoglossa* will be quite clearly defined. Plastid symbiosis probably first appeared in *Volvatella* among the epifaunal forms, such as *V. bermudae* and *V. viridis*. For some reason, plastid symbiosis was lost along the *Lobiger-Oxynoe* lines, and in the Juliidae, accompanied by reduction in the pallial diverticula, but was further refined in the Elysiidae. Interestingly, the pallial diverticula are present in the burrowing *V. laguncula* (Thompson, 1979), but apparently do not extend into the anterior of the mantle. Of course, plastid retention in burrowing forms would have no value, because no light would reach the plastids while submerged in the sediment.

Thompson (1979) suggests that the genus *Volvatella* represents a primarily infaunal form which, together with *Ascobulla*, links the burrowing cephalaspidiiform opisthobranchs and the more advanced epifaunal tectibranch ascoglossans, *Oxynoe* and *Lobiger*. He based this idea on observation of *V. laguncula*, which burrows several cm below the surface of muddy sand. However, my own observations on living *Ascobulla ulla* (Marcus and Marcus, 1970), from Fort Pierce, Florida, and on *V. bermudae*, suggest a slight modification of this view. *Ascobulla ulla* also burrows in fine, well-compacted sand, but frequently emerges and crawls up into overlying growths of *Caulerpa racemosa*. Possibly *V. laguncula* also emerges occasionally, especially at night. *V. bermudae* seems to require very high quality, well-oxygenated water, in contrast with Thompson's (1979) belief that *V. laguncula* pumps a fine ooze of mud through its mantle cavity. Some other *Volvatella* species also seem to be truly epifaunal, while others, described as typical components of the *Caulerpa* community (Burn, 1966; Hamatani, 1972; 1976) are at least intermittently epifaunal.

Volvatella viridis is green in color, as is *V. bermudae*, which would be valueless as cryptic coloration for infaunal forms, but quite advantageous for epifaunal forms which are intimately associated with algae. There are other *Volvatella*

species of white or yellow color (Thompson, 1979) and these perhaps burrow intermittently, similar to *V. laguncula*. The degree of development of Hancock's organ also appears to correlate with color and burrowing behavior. *V. vigourouxii* has a rudimentary Hancock's organ (a structure associated with burrowing) (Baba, 1966); *V. bermudae*, however, does not. Thus, *Ascobulla* exhibits an early tendency of primarily infaunal, but intermittently epifaunal, behavior. This behavior diverges in the genus *Volvatella*, which ranges from primarily infaunal to fully epifaunal habitats, matching those of *Oxynoe* and *Lobiger*.

Another characteristic shared by *V. laguncula* and *Ascobulla ulla* is the rhythmic adduction of the shell (Thompson, 1979; Marcus and Marcus, 1956). The strong ciliation of the mantle cavity seemingly obviates the need for pumping movements of the shell, as suggested by Thompson (1979). Also, there is no identifiable valve mechanism, which should be present if this movement functions in ventilation of the mantle cavity. An alternative explanation is that the "pumping" movements of the shell might assist in burrowing in compact sand. Both species have shells which gently taper anteriorly, and the passive relaxation of the shell may loosen sediment surrounding the shell, coincidentally increasing the availability of interstitial water from the surrounding sediment for respiration.

ACKNOWLEDGMENTS

This research was supported by the Samuel Riker Fellowship of the Bermuda Biological Station, and by NSF Grant DEB 7815449. I thank K. Jensen for her comments and ideas. I am also very grateful to Dr. W. Sterrer for sharing his extensive knowledge of collecting sites in Bermuda, and to H. Stirts for his micrograph of plastids in *V. bermudae*. This publication is contribution No. 840 of the Bermuda Biological Station.

LITERATURE CITED

- Baba, K. 1966. Gross anatomy of the specimens of the shelled sacoglossan *Volvatella* (= *Arthessa*) collected from Okino-Erabu Island, southern Kyushu, Japan (Nudibranchia). Publ. Seto Mar. Biol. Lab. 14: 197-205.
- Boettger, C. R. 1963. Gastropoden mit zwei Schalenklappen. Verhandl. dt. Zool. Ges. Wein (1962): 403-409.
- Burn, R. 1966. The opisthobranchs of a Caulerpan microfauna from Fiji. Proc. Malac. Soc. Lond. 37: 45-65.
- Clark, K. B., and M. Busacca. 1978. Feeding specificity and chloroplast retention in four tropical Ascoglossa, with a discussion of the extent of chloroplast symbiosis and the evolution of the order. J. Moll. Stud. 44: 272-282.
- Evans, T. J. 1950. A review of Pease's genus *Volvatella*, together with a preliminary report on a new sacoglossan genus. Proc. Malac. Soc. Lond. 28: 102-106.
- Hamatani, I. 1972. A new species of *Volvatella* Pease, 1860, found in the "Caulerpan Microfauna" in the province of Kii, Middle Japan (Opisthobranchia: Sacoglossa). Publ. Seto Mar. Biol. Lab. 21: 13-20.
- . 1976. Preliminary account of a new species of *Volvatella* Pease, 1860, *V. viridis* sp. nov., found in the caulerpan microfauna in Japan (Opisthobranchia: Sacoglossa). Publ. Seto Mar. Biol. Lab. 22: 371-376.
- Kay, E. A. 1961. A new opisthobranch mollusc from Hawaii. Pacif. Sci. 15: 112-113.
- . 1968. A review of the bivalved gastropods and a discussion of evolution within the Sacoglossa. Symp. Zool. Soc. Lond. 22: 109-134.
- Marcus, E., and E. dB. R. Marcus. 1956. On the tectibranch genus *Cylindrobulla*. Anais Acad. Brasil. Ciencias 28: 119-128.
- , and ———. 1970. Opisthobranchs from Curaçao and faunistically related regions. Stud. Fauna Curaçao 33: 1-129.
- Pease, W. H. 1860. Descriptions of new species of Mollusca from the Sandwich Islands. Proc. Zool. Soc. Lond. 28: 18-37.
- . 1868. Descriptions of marine gasteropoda, inhabiting Polynesia. Am. J. Conch. 4: 71-90.
- Stirts, H. M. 1980. Chloroplast symbiosis in tectibranch molluscs (Opisthobranchia: Gastropoda). Ph.D. Dissertation, Florida Institute of Technology, Melbourne. 96 pp.

Thompson, T. E. 1979. Biology and relationships of the South African sacoglossan mollusc *Volva-tella laguncula*. J. Zool., Lond. 189: 339-347.

DATE ACCEPTED: August 4, 1980.

ADDRESS: *Department of Biological Sciences, Florida Institute of Technology, Melbourne, Florida 32901.*